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Podosphaerasteridae fam. nov. (Echinodermata: Asteroidea: Valvatida), with a New Species, *Podosphaeraster toyoshiomaruae*, from Southern Japan

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A new family, Podosphaerasteridae, is proposed for the valvatid asteroid genus *Podosphaeraster*, with a new species of the genus from southern Japan, western North Pacific. *Podosphaeraster* differs from the fossil genus *Sphaeraster* and other valvatid families by the overall body form and the skeletal structure. The new Japanese species, *P. toyoshiomaruae* sp. nov., differs from the previously known species of *Podosphaeraster* principally in number and size of granules on the abactinal and actinal plates, number of adambulacral spines, retention of perforations in terminal plates, and ratio of horizontal diameter to vertical diameter. *Podosphaeraster toyoshiomaruae* was collected together with abundant sponges and probably lives closely associated with sponge. This is the first record of the genus *Podosphaeraster* from Japanese waters.
Key Words: *Podosphaeraster toyoshiomaruae*, Podosphaerasteridae, Sphaerasteridae, Asteroidea, Japan, new family, new species, sponge

Introduction

The genus *Podosphaeraster* was described by A. M. Clark in Clark and Wright (1962) for the new species *P. polyplax* A. M. Clark in Clark and Wright, 1962 as an unusual sea-star of spherical-form with abactinal and actinal plates arranged in horizontal, rather than longitudinal, series and with no apparent ambital margin. Clark and Wright (1962) believed that *Podosphaeraster* and the Jurassic *Sphaeraster* Quenstedt, 1875 have close phylogenetic affinities, and they assigned *Podosphaeraster* to the family Sphaerasteridae Schöndorf, 1906. This family, comprising *Podosphaeraster*, *Sphaeraster*, and the Cretaceous *Valettaster* Lambert, 1914, is considered to belong in the order Valvatida (Clark and Wright 1962; Spencer and Wright 1966; Blake 1984, 1987, 1989). Blake (1984) re-examined in detail the skeletal structure of *Sphaeraster* and concluded that the fossil genus did not share "close phylogenetic affinities" with *Podosphaeraster* and that the two genera should be referred to separate families within the order Valvatida, but he did not assign *Podosphaeraster* to a new family. Cherbonnier (1970), Rowe and Nichols

(1980), Rowe *et al.* (1982), and Rowe (1985) followed the descriptive format of Clark and Wright (1962) when describing new species of *Podosphaeraster* and reviewing the gross external and internal anatomy of this enigmatic genus. In addition, though, Rowe (1985) included a detailed argument for recognizing longiseries of abactinal and actinal plates as well as a row each of supero- and inferomarginal plates, between which latter rows he identified intermarginal plates (see Fig. 1). Rowe (1985) did not discuss the phylogenetic implications of this interpretation; unaware of Blake's (1984) conclusions, but equivocal about the relationships between *Podosphaeraster*, *Sphaeraster*, and *Valettaster*, he maintained *Podosphaeraster* within the Sphaerasteridae. Rowe (1985) included a discussion of the current apparently disjunct distribution (Western Pacific and Northeastern Atlantic) of the genus *Podosphaeraster*, concluding that this may have come about from a formerly pan-Tethyan distribution as a result of subsequent vicariance events. He suggested that *Podosphaeraster* may be an early Tertiary (if not late Cretaceous) genus despite lacking fossil representatives. Rowe (1985) further predicted that *Podosphaeraster* would be found more widely, including in the Indian Ocean. Finally, Blake (1987: 523), responding to unpublished comments made to him by A. M. Clark regarding affinities between *Podosphaeraster* and the deep-sea asteroid family Caymanostellidae Belyaev, 1974, concluded that the similarities are due to convergence. Despite his earlier comments (Blake 1984), Blake (1987, 1989) retained without comment the genus within the family Sphaerasteridae in the order Valvatida, placing the Caymanostellidae in the order Velatida.

We firmly support Blake's (1984) conclusion regarding the distant, at best, affinities of *Podosphaeraster* with fossil genera and take the further step of describing a new family to accommodate this genus. We also describe a new species of *Podosphaeraster* based on six specimens collected from off southern Japan; this is the first reported occurrence in Japanese waters. Finally, we also comment on taxonomical differences among the currently known species included in the genus.

In establishing the new taxa we have, for taxonomic consistency, followed Clark and Wright's (1962) lead by describing abactinal and actinal plates in horizontal alignment; we believe, however, that our new interpretation of the limits and extent of the apical system (see p. 328 and Fig. 1) is not only taxonomically important, but lends credence to Rowe's (1985) proposal regarding asteroid plate arrangement and plate homology between *Podosphaeraster* and other members of the class Asteroidea. We have included this alternative description of plate arrangement for future phylogenetic consideration.

Materials and Methods

The new specimens were collected by an ORI-type biological dredge of 0.5 m span with a mesh size of 5 mm deployed by the T/S *Toyoshio Maru* of Hiroshima University. The collected specimens were fixed with buffered 10% sea-water formalin on board and later transferred to *c.* 75% ethanol for preservation, or directly put into *c.* 75% ethanol. One specimen was dried for close examination of ossicles. Photographs were taken of formalinized, alcoholic, and dried specimens. Another specimen was partly dissected for examination of internal structure. Standard paraffin sections were stained with hematoxylin and eosin stain to examine histol-

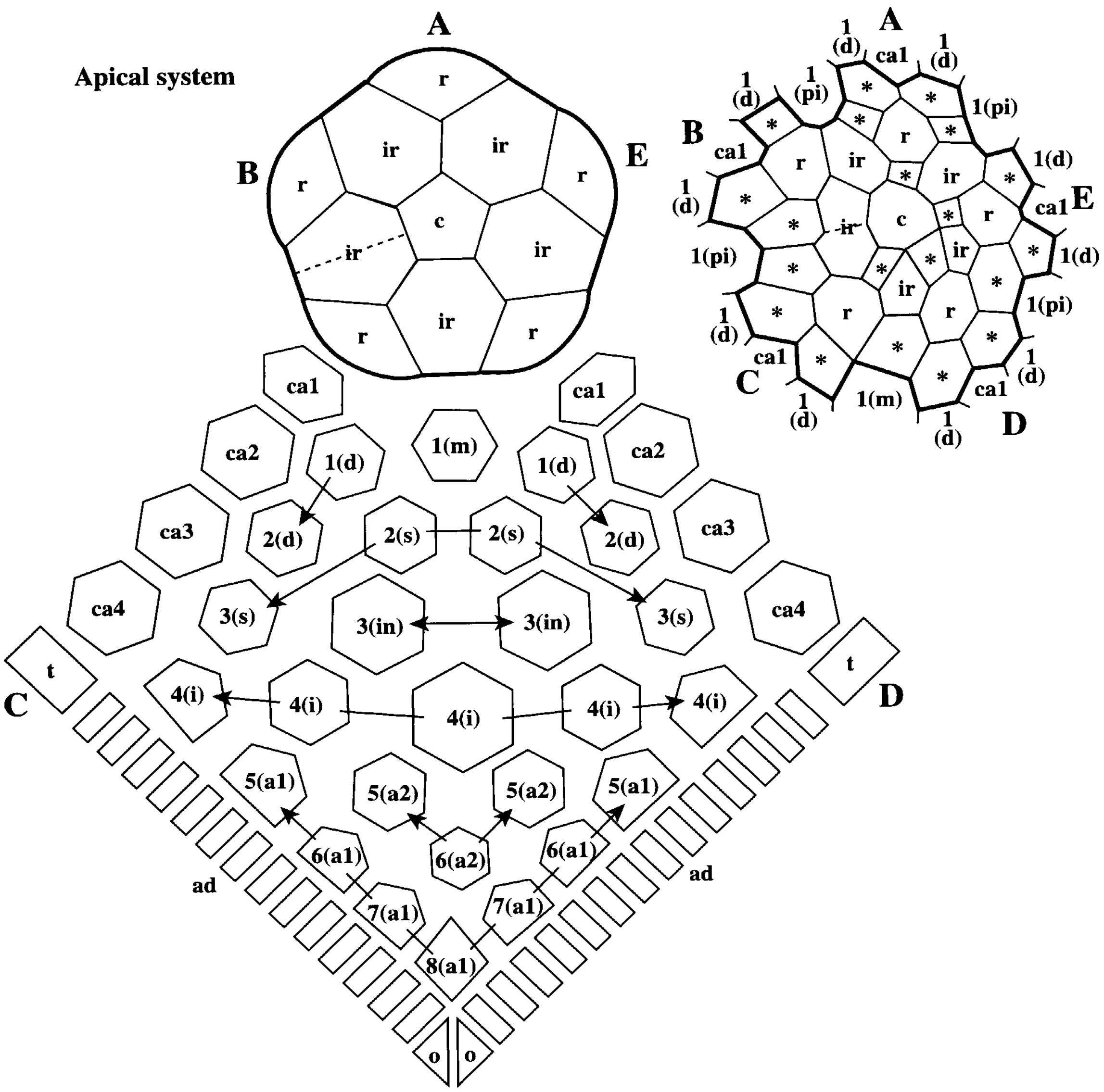

Fig. 1. Diagrammatic view of basic arrangement of skeletal plates of *Podosphaeraster* (modified from Rowe 1985, fig. 2) and combining notations contrasting horizontal alignment of skeletal plates (after Clark and Wright 1962) with longiseries and marginal alignment of plates (after Rowe 1985). Variation of apical system (outline enhanced for clarity) with additional plates (indicated by asterisks) is also shown (from holotype of *P. polyplax*, after Clark and Wright 1962, fig. 2). Bisecting longitudinal furrow of BC interradial plates shown by broken lines. A–E, radii after Carpenter's (1884) system. Apical system: c, central plate; ir, interradial plate; r, radial plate; *, additional plate. Abactinal and actinal plates: ad, adambulacral plate; ca1–ca4, carinal plates 1–4; o, oral plate; t, terminal plate; 1–8, horizontal rows of plates (1–3, rows of abactinal plates; 4, row of sub-ambital plates; 5–8, rows of actinal plates). Alternative interpretation of plates shown in parentheses and members of longiseries linked by arrows: a1–a2, actinolateral plates; d, dorsolateral plate; i, inferomarginal plate; in, intermarginal plate; m, madreporic plate; pi, primary interradial plate; s, superomarginal plate.

ogy of the dissected gonad. Scanning electron microscopy (SEM) observations with a Jeol JSM 5200LV were made on freeze-dried preparations of the dissected tube feet, which were sputter-coated with gold-palladium.

The body size was measured by horizontal diameter (HD) and vertical diameter (VD) instead of major (R) and minor (r) radii usually used in asteroids because of the spherical form of the body. Each radius and interradius is denoted by the letters A–E according to Carpenter's (1884) notation. The specimens have been deposited in the National Science Museum, Tokyo (NSMT).

Taxonomic Account

Podosphaerasteridae fam. nov.

(New Japanese name: mari-hitode-ka)

Diagnosis. Small (HD up to 21.5 mm), subspherical (HD/VD=1.08) to cushion-shaped (HD/VD=1.82 [?2.2, see Table 2]) valvatid asteroids. Skeletal plates polygonal (mostly hexagonal) except for rhomboidal adambulacral plates, closely abutting except at points pierced by isolated abactinal and actinal papulae. Plates not supported internally. Abactinal and actinal plates distinctive, bounded within diamond-shaped interradial area delimited aborally by apical system of plates, orally by paired oral plates, and laterally by carinal and adambulacral plates of adjacent radii. Abactinal and actinal plates apparently arranged in 8 horizontal rows; 3 rows each of 3, 4, 4 abactinal plates, sub-ambital row of 5–8 plates, and 4 rows each of 4, 3, 2, 1 actinal plates. According to alternative interpretation, abactinal and actinal plates aligned in longiseries, separated by marginal plates as follows: prominent primary interradial plate with single row of 2 dorsolateral plates on either side; actinal plates in 2 series forming 2 chevrons below 5–8 sub-ambital inferomarginal plates; and 4 superomarginals in arched series above ambitus with 2 intermarginal plates between marginal series (Fig. 1). Apical system of central, interradial, and radial plates distinct, with at least one interradial plate in interradius BC bisected by shallow, longitudinal furrow. Some additional plates present or absent in apical system (Fig. 1). Madreporite simple, piercing center of middle plates of most proximal horizontal row of abactinal plates in interradius CD. Rows of 4 radial carinal plates extending between apical system and each terminal plate. Terminal plates perforated or not. Armament of skeletal plates granuliform or short spiniform. Pedicellariae lacking. Internal wall of test reinforced in each mid-interradius by calcite ridge; each ridge supporting diaphanous mesentery extending to about half width of central axis, incompletely dividing body cavity into 5 partitions. Each mesentery supporting gonad aborally. Digestive system highly modified, with reduced cardiac stomach, complex pyloric structure, and rectal canal with or without rectal caecae.

Type genus. *Podosphaeraster* A. M. Clark (in Clark and Wright 1962)

Other genera. Currently none.

Remarks. We find sufficient strength of reason in Blake's (1984) contention that apparent similarities between *Podosphaeraster* and *Sphaeraster* have been developed convergently, that we formally recognize and describe the family Podosphaerasteridae for that nominal genus. Sphaerasteridae are herein restricted to only the extinct genera *Sphaeraster* and *Valettaster*. These fossil starfishes are

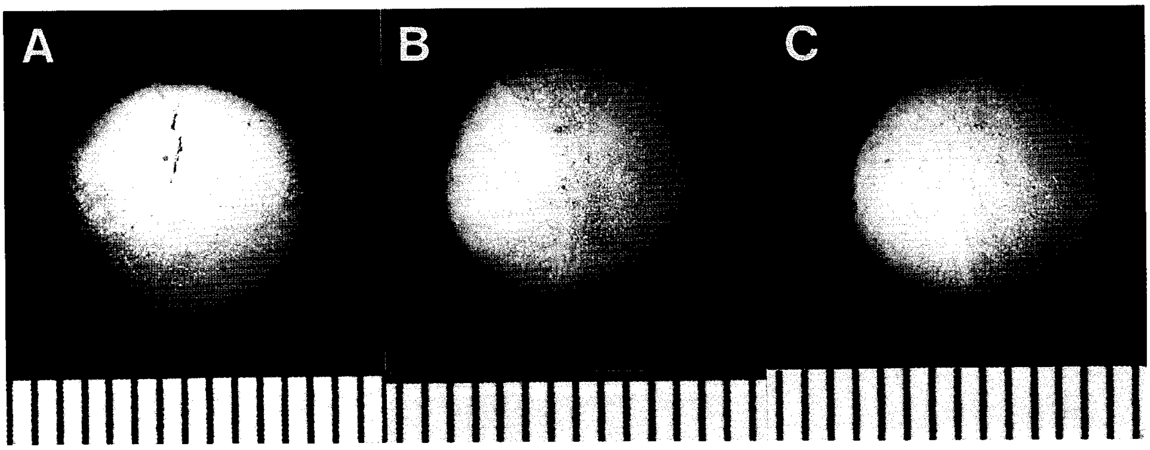

Fig. 2. *Podosphaeraster toyoshiomaruae* sp. nov., holotype (NSMT E-4162). Photographs in alcohol. A, dorsal view; B, ventral view; C, lateral view. One graticule: 1 mm.

actinally flat and abactinally domed in shape and relatively large (exceeding 10 cm in horizontal diameter) (Schöndorf 1906a, b; Spencer and Wright 1966), thus, completely different from the smaller and spherical *Podosphaeraster*. *Podosphaeraster* has a relatively constant arrangement of skeletal plates (Fig. 1) without the conspicuous marginal plates seen in *Sphaeraster*. We consider that the affinities of the Podosphaerasteridae lie with the Goniasteridae Forbes, 1941 (*s. str.*) and Asterodiscididae Rowe, 1977 in the superfamily Goniasteroidea Forbes, 1941, as, in effect, Blake (1987, 1989) has already concluded by including *Podosphaeraster* within his wider view of the Sphaerasteridae. It is clear from the overall body form, skeletal plate arrangement, and distinctive form of the digestive system that the Podosphaerasteridae is distinct from the Goniasteridae, Asterodiscididae, and Sphaerasteridae (*s. str.*). The digestive system is a feature useful for recognizing families according to Jangoux (1982).

Genus ***Podosphaeraster*** A. M. Clark, 1962
(New Japanese name: mari-hitode-zoku)

Podosphaeraster A. M. Clark in Clark and Wright 1962: 243–244; Spencer and Wright 1966: U55; Cherbonnier 1970: 206; Rowe and Nichols 1980: 289–291; Rowe *et al.* 1982: 83–84, 87–88, 92; Rowe 1985: 309–310; Clark and Downey 1992: 225–226.

Diagnosis. The same as for the family.

Type species. *Podosphaeraster polyplax* A. M. Clark, 1962, by original designation.

Podosphaeraster toyoshiomaruae sp. nov.
(New Japanese name: toyoshio-mari-hitode)
(Figs 2–9)

Material examined. Six specimens were collected at Oshima-shinsone, about 39 km north of Amami-Oshima Island, southern Japan. Holotype: NSMT E-4162;

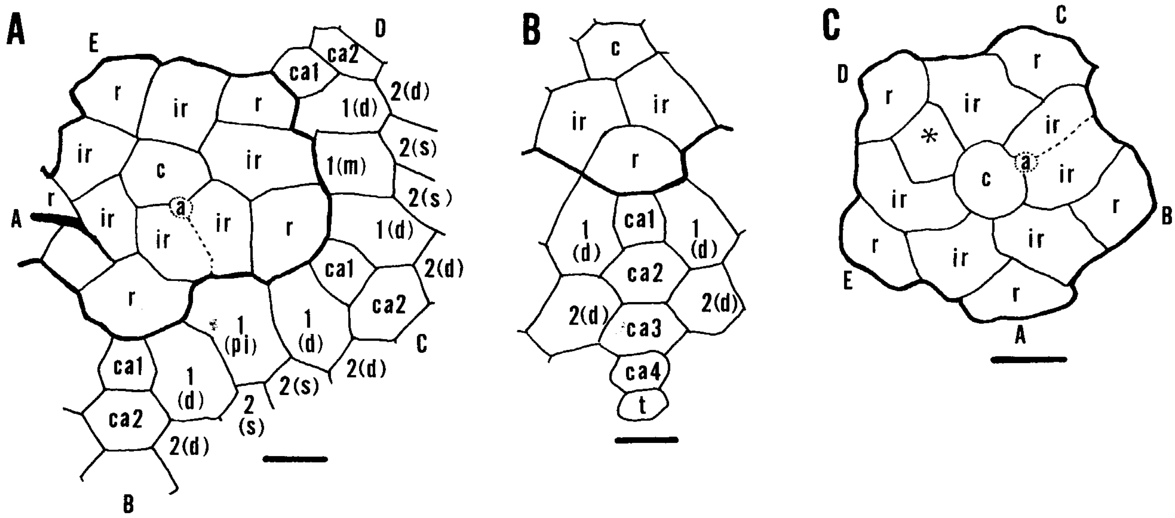

Fig. 3. *Podosphaeraster toyoshiomaruae* sp. nov.: A–B, holotype (NSMT E-4162); C, paratype (NSMT E-4165). A, apical system and some surrounding plates, one interradial and one radial plate cracked accidentally; B, carinal plates of radius D; C, apical system. Plate arrangement, with outline of apical system enhanced for clarity. Bisecting longitudinal furrow of BC interradial plates shown by broken lines. Alternative interpretation of plates shown in parentheses. A–E, radius number according to Carpenter's (1884) system; a, anus; c, central plate; ca1–ca4, carinal plates 1–4; d, dorsolateral plate; ir, interradial plate; m, madreporic plate; pi, primary interradial plate; r, radial plate; s, superomarginal plate; t, terminal plate; *, additional plate; 1–2, rows of abactinal plates. Scale bars: 1 mm.

28°52.52′N, 129°33.13′E, 158 m deep, 29 May 1999. Three paratypes: NSMT E-4163 (partly dissected), NSMT E-4164 (dried), NSMT E-4165; the same site, 153–170 m deep, 30 May 2000. Two paratypes: NSMT E-4568, NSMT E-4569; 28°52.54′N, 129°33.11′E–28°52.68′N, 129°33.21′E, 145 m deep, 28 May 2001.

Diagnosis. Known HD between 3.9 and 12.2 mm; almost spherical form with HD/VD of 1.08–1.21; apical system usually having 1 central, 5 interradial, and 5 radial plates; carinal row of 4 abutting flat plates; terminal plate losing perforation with growth; actinal and abactinal plates with maximum of 15–36 short granules; 8–17 adambulacral plates with 3–5 furrow spines and 2–7 subambulacral spines each; oral plates with 4–6 furrow spines and 3–6 suboral spines each.

Description of holotype. Body almost spherical in form (Fig. 2) with HD of 10.0 mm (i.e., R=5 mm) and VD of 9.2 mm. HD/VD 1.1. Spherical body formed by thick, abutting, polygonal plates. Single papulae emerging between plates. Plates bearing up to 30 spaced, granulate, easily detached spines; spines cylindrical or slightly tapering, mostly 0.14–0.24 mm in height, 0.07–0.18 mm in width. Length of spines on abactinal plates almost same as length of those on actinal plates.

In apical system, central plate surrounded by 5 interradial plates (Fig. 3A). Interradial plate in interradius BC cleft radially. Anus lying on suture between central plate and interradial BC, surrounded by 6 spines (Fig. 4A). Wedge-shaped radial plate occurring in each distal angle between adjacent interradials.

Row of 4 carinal plates along each dorsal radius contacting proximally with wedge-shaped radial plate of apical area and distally with terminal plate (Fig. 3B).

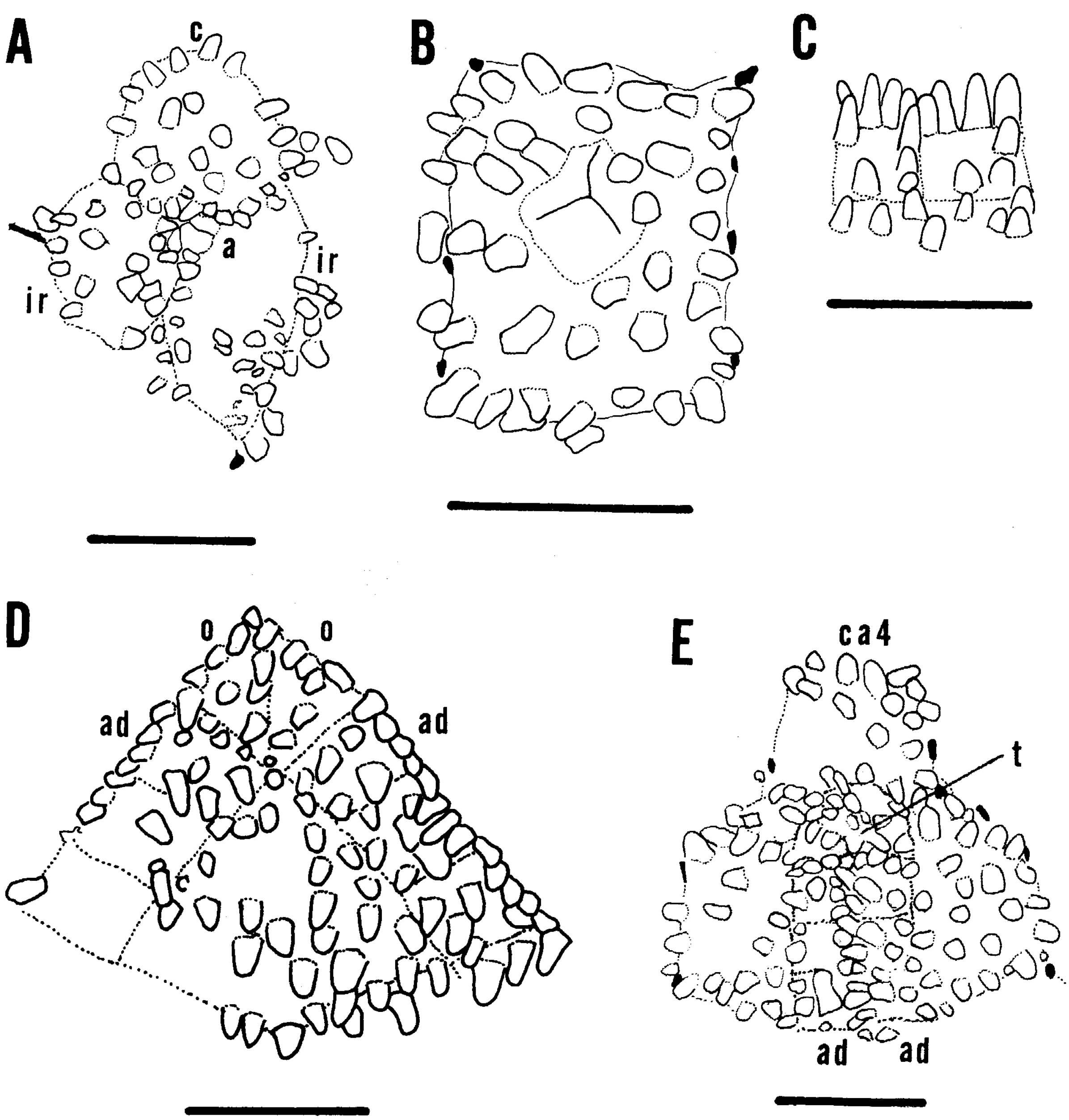

Fig. 4. *Podosphaeraster toyoshiomaruae* sp. nov., holotype (NSMT E-4162). A, anus surrounded by central plate and interradial plate bisected by furrow; B, madreporic plate; C, tenth (right) and 11th (left) adambulacral plates; D, mouth angle; E, terminal plate and surrounding plates. a, anus; ad, adambulacral plate; c, central plate; ca4, carinal plate 4; ir, interradial plate; o, oral plate; t, terminal plate. Scale bars: 1 mm.

First carinal elongate, rather bell-shaped; other three carinals hexagonal, wider than long. Madreporic plate situated in interradius CD (Fig. 3A), almost rectangular in shape, having raised bump with tri-radiated grooves (Fig. 4B).

Ambulacral grooves lined by 13 square adambulacral plates on each side. Each plate bearing usually 4 (rarely 5) furrow spines on adradial edge and about 3–6 subambulacral spines on flat surface (Fig. 4C–D). Pair of triangular oral plates present in each oral angle; each plate bearing 5–6 oral spines and about 3–4 suboral spines.

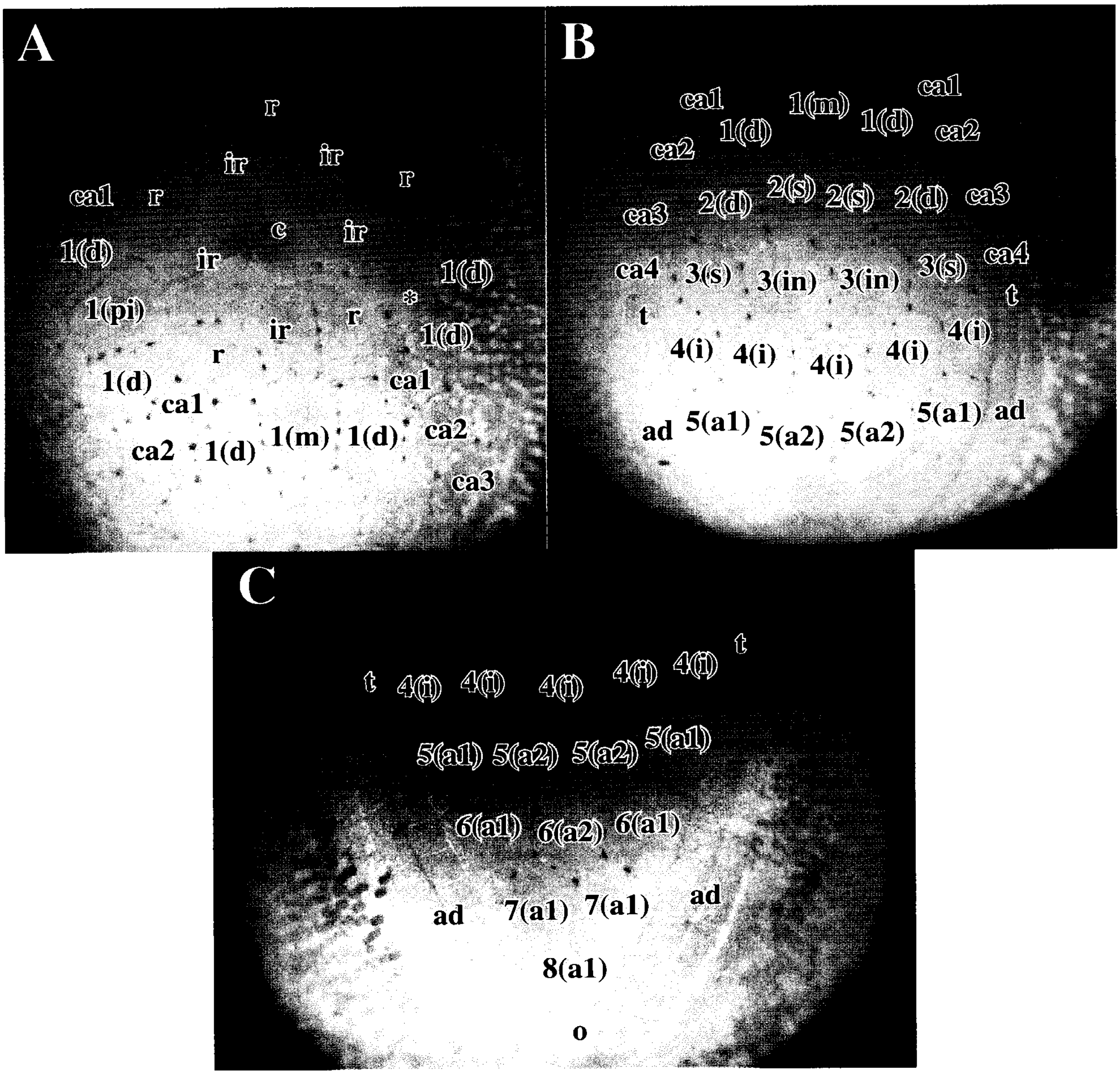

Fig. 5. *Podosphaeraster toyoshiomaruae* sp. nov., paratype (NSMT E-4164). Plate arrangement of apical part and interradius CD. A, top view; B, lateral view; C, ventrolateral view. ad, adambulacral plate; c, central plate; ca1–ca4, carinal plate 1–4; ir, interradial plate; o, oral plate; r, radial plate; t, terminal plate; *, additional plate; 1–8, horizontally aligned rows of test plates (1–3, abactinal plates; 4, sub-ambital plates; 5–8, actinal plates). Alternative interpretation of plates shown in parentheses: a1–a2, actinolateral plates; d, dorsolateral plate; i, inferomarginal plate; in, intermarginal plate; m, madreporic plate; pi, primary interradial plate; s, superomarginal plate.

First actinal plate abutting three adambulacral plates. Terminal plates oval or hemispherical, elevated centrally (Fig. 4E). Terminal plate in radius D possessing small perforation; other terminal plates lacking any perforation. Terminal tube-feet protruding either through terminal plate perforation or from under inperforate terminal plates.

Plates in the interradial abactinal and actinal triangles comprising typically 8

more-or-less horizontal rows; 3 rows each of 3, 4, 4 abactinal plates, sub-ambital row of 5 plates, and 4 rows each of 4, 3, 2, 1 actinal plates (for alternative interpretation of plate arrangement in this family, see p. 320 and Fig. 1).

Body color almost white when alive, remaining in formalin and alcohol.

Notes on paratypes. The range in size, number of plates, and number of spines are shown in Table 1. The arrangement of the skeletal plates is shown for the dried paratype (NSMT E-4164, HD 9.0 mm) (Fig. 5). The apical plates are similar to those of the holotype, except that there is one additional plate in interradius BC. The plates in the interradial abactinal and actinal triangles are also similar to those of the holotype. The sub-ambital row of five plates extends between the two adjacent terminal plates in interradius CD, but in the other interradii, there are six plates with two small, oval, and obliquely aligned plates centrally placed in the row. In another paratype (NSMT E-4615), the apical system similarly contains an additional plate in interradius DE (Fig. 3C). In this paratype also, in all interradii the number of plates in the sub-ambital row is six, with the central two plates small, oval, and obliquely aligned.

The perforation in the terminal plates opens up with growth. The largest paratype (NSMT E-4163, HD 12.2 mm) and the holotype (HD 10.0 mm) have only one

Fig. 6. *Podosphaeraster toyoshiomaruae* sp. nov., terminal plates of paratypes. A, NSMT E-4164, radius A; B, NSMT E-4164, radius D; C, NSMT E-4569, a radius.

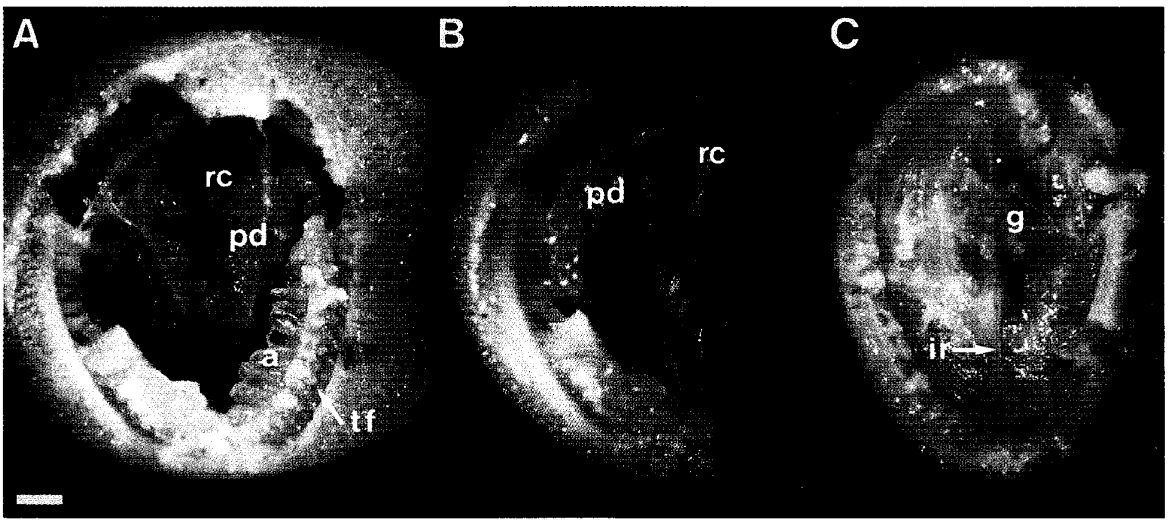

Fig. 7. *Podosphaeraster toyoshiomaruae* sp. nov., largest paratype (NSMT E-4163). A–B, dissected interradius CD; C, internal view of interradius CD. a, ampulla; g, gonad; ir, interradial ridge; pd, pyloric diverticula; rc, rectal caeca; tf, tube foot. Scale bar: 1 mm.

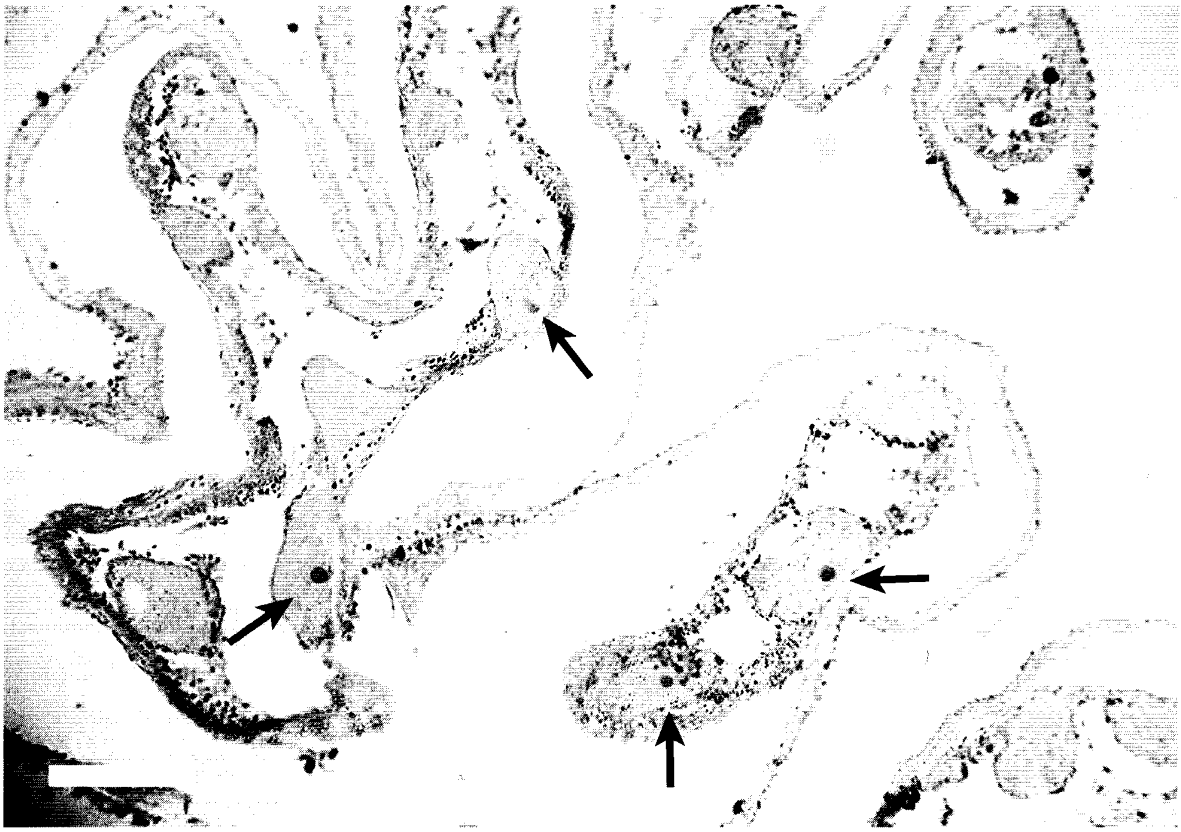

Fig. 8. *Podosphaeraster toyoshiomaruae* sp. nov., largest paratype (NSMT E-4163). Histological section of gonad showing oocytes (indicated by arrows).

perforated terminal plate in radius D and E, respectively. The medium-sized paratype (NSMT E-4164) has a large perforation evident in the terminal plate of radius C, small perforations in radii D and E, but no perforation in radii A and B (Fig. 6A–B). The smaller paratypes (HD 3.9–8.4 mm) have all 5 terminal plates perforated. The apparent opening of the terminal plate perforation with growth leads to the displacement of the associated tube-foot from its position through the plate perforation to its position under the terminal plate [cf. *P. gustavei*, see Rowe (1985)]. The terminal plate of the smallest paratype (NSMT E-4569) has a slightly curved horizontal row of eight relatively flat spines under the perforation (Fig. 6C).

The color is light-greenish brown (NSMT E-4163, 4568) with several brownish spots (NSMT E-4165, 4569). The terminal plates and several plates on the dorsal side have brownish skin (NSMT E-4164), and the brownish color remains faintly in alcohol.

In the partly dissected paratype (NSMT E-4163), the ossicles are about 0.5 mm thick. The pyloric diverticula are well developed, and five conspicuous, pouch-like rectal caecae are present (Fig. 7A–B). The inner wall of the test is reinforced by an interradial ridge in each interradial midline, and a lobulate gonad is attached aborally to the interradial mesentry (Fig. 7C). Histological examination of the lobulate gonad shows this specimen to be female, and the gonad is almost hollow with only a few small oocytes (Fig. 8). A single large ampulla is positioned on top of each tube

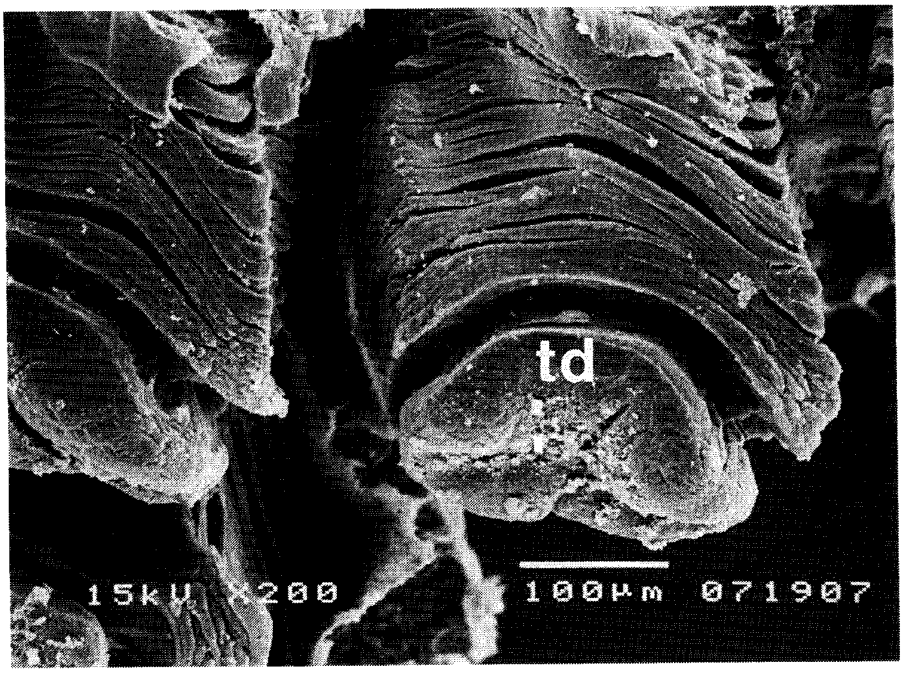

Fig. 9. *Podosphaeraster toyoshiomaruae* sp. nov., largest paratype (NSMT E-4163). SEM photo of contracted tube feet with terminal suckered disc (td).

foot (Fig. 7A), and the tube feet each have a small, terminal sucker disc (Fig. 9).

Etymology. The specific name *toyoshiomaruae* is derived from the training ship *Toyoshio Maru*, as the specimens were collected during the cruises of this ship. As for the Japanese names, "mari" means a kind of ball which is originally used for "ke-mari", a traditional football game in Japan, "hitode" means a sea-star, and "ka" and "zoku" denote taxonomic ranks of family and genus, respectively.

Discussion

Comparison with other species. The genus *Podosphaeraster* currently includes four valid species: *P. polyplax* A. M. Clark, 1962 (type species) and *P. pulvinatus* Rowe and Nichols, 1980 from the West Pacific, and *P. thalassae* Cherbonnier, 1970 and *P. gustavei* Rowe, 1985 from the North-east Atlantic, although Clark and Downey (1992) have suggested that *P. gustavei* is conspecific with *P. thalassae*.

The morphometric data recorded in Table 1 clearly show changes with growth in the six present specimens of *P. toyoshiomaruae*, ranging in HD from 3.9–12.2 mm. The new species differs clearly from the Atlantic species *P. thalassae* and *P. gustavei* principally in having larger numbers of shorter granules/spines at comparative body sizes (Table 2), but it is interesting to note that both *P. toyoshiomaruae* and *P. gustavei* possess similar internal gross morphology (Table 2; Rowe 1985). Also, *Podosphaeraster toyoshiomaruae* and the two Atlantic species (Cherbonnier 1970; Rowe 1985) retain perforations in terminal plates until *c.* 8.4 mm and *c.* 5.6–6 mm in HD, respectively, and lose them with further growth. The other West-Pacific species, *P. polyplax* and *P. pulvinatus*, retain the terminal plate

Table 1. Comparison in numerical characteristics among the specimens of *Podosphaeraster toyoshiomaruae* sp. nov.

Specimen no. (NSMT E-)	4163 paratype	4162 holotype	4164 paratype	4165 paratype	4568 paratype	4569 paratype
Horizontal diameter (HD, mm)	12.2	10.0	9.0	8.4	7.0	3.9
Vertical diameter (VD, mm)	10.7	9.2	8.3	7.2	6.2	3.3
HD/VD ratio	1.14	1.09	1.08	1.16	1.14	1.21
Granule number per plate	<*c.* 36	<*c.* 30	<*c.* 28	<*c.* 25	<*c.* 22	<*c.* 15
Abactinal granule length (mm)	<0.24	<0.24	<0.22	<0.18	<0.15	<0.14
Actinal granule length (mm)	<0.24	<0.23	<0.19	<0.15	<0.12	<0.12
Adambulacral plate number	17	13	14	13	11	8
Furrow spines, number per plate	4–7 (distally 2–3)	4 (rarely 5)	4 (distally 2–3)	4	3–4	3
Subambulacral spines, number per plate	5	3–6	4 (rarely 2–6)	3–5	4	2–3
Oral spine number	4–6	5–6	5–6	5	4–5	4
Suboral spine number	3–4	3–4	3–5	4	4 (rarely 3–5)	3–4
Perforations in terminal plates	1	1	3	5	5	5

perforation even in the largest-size specimens available (15 mm and 21.5 mm HD, respectively) (Rowe and Nichols 1980; Rowe *et al.* 1982).

Podosphaeraster toyoshiomaruae can be readily distinguished from its closest geographical neighbor, *P. polyplax*, which is distributed in the South China Sea, Arafura Sea, and in the Loyalty Islands. Firstly, the skeletal plates of *P. polyplax* bear far fewer granules/spines at comparative sizes. Secondly, in *P. polyplax*, the apical system appears to have an extended, more complex plate arrangement. Re-examination of a specimen (Australian Museum J11720, HD=11.5 mm) from the Arafura Sea shows that the apical system is actually more extensive than shown by Rowe *et al.* (1982, fig. 2C), since it includes an outer ring of ten plates in five pairs. This arrangement is similar to that in the holotype (HD=12 mm) from the South China Sea (c.f. Clark and Wright 1962, fig. 1; Rowe *et al.* 1982, fig. 2D; Fig. 1 herein); however, in the two specimens (Australian Museum J11721) from the Loyalty Islands also recorded by Rowe *et al.* (1982), one (HD=15 mm) has a simple, stellate apical system, whereas the second specimen (HD=9.5 mm) has three small additional plates in the apical system. Whether such differences between apical systems call for recognition of a new taxon for the Loyalty Islands specimens needs further consideration when more comparative material become available. Thirdly, following dissection and examination of the internal morphology of the holotype of *P. polyplax*, we can confirm that none of the specimens identified as *P. polyplax*

Table 2. Summary of comparative features of *Podosphaeraster* species. Measurements in square brackets not only from original description but also from subsequent works.

Species name	*P. polyplax*	*P. pulvinatus*	*P. toyoshiomaruae*	*P. thalassae*	*P. gustavei*
Number of known specimens	1 [4]	2	6	2 [7]	4
Horizontal diameter (HD, mm)	12.0 [9.5–15.0]	12.75–21.5	3.9–12.2	6.0–8.5 [6.0–9.0]	5.6–14
Vertical diameter (VD, mm)	11.0 [7.5–13.25]	5.75–11.8	3.3–10.7	5.0–7.4	4.5–12.7
HD/VD ratio	1.1 [1.1–1.26]	1.82–?2.2*	1.08–1.21	1.15–1.2	1.1–1.5
Apical system	irregular >10 plates	regular 10 plates	regular 10 plates	regular 10 plates	regular 10 plates
Proximal carinal plates	flat	flat	flat	small, nodular in 3 radii	flat
Granule number per plate	10–12	>20	15–36	4–8	4–8
Abactinal granule length (mm)	*c.* 0.25	0.22–0.265	0.14–0.24	*c.* 0.45**	0.27–0.38
Actinal granule length (mm)	*c.* 0.25	0.35–0.475	0.12–0.24	*c.* 0.75**	0.36–0.45
Adambulacral plate number	21	16–21	8–17	15–18	10–20
Furrow spines number per plate	2–3	3	3–7	2–3	2–3
Subambulacral spines, number per plate	2	2–4	2–6	2	2
Oral spines number	3	3	4–6	3	3
Suboral spine number	1	2–3	3–5	2	2–3
Perforation in terminal plates	remain in larger animals	remain in larger animals	lost in larger animals	lost in larger animals	lost in larger animals
Rectal caecae	absent	unknown	present	unknown	present
Distribution (depth)	West Pacific; Loyalty Islands (85–100 m), Arafura Sea (125 m), South China Sea (72–90 m)	West Pacific; Guam (244–324 m), Loyalty Islands	West Pacific; southern Japan (145–170 m)	Eastern North Atlantic; off Bay of Biscay (500–520 m)	Eastern North Atlantic; off Bay of Biscay (500–615 m); Azores (500–520 m)
References	Clark and Wright 1962; Rowe and Nichols 1980; Rowe *et al.* 1982	Rowe and Nichols 1980	Present study	Cherbonnier 1970, 1974; Clark and Downey 1992	Rowe 1985

* Damaged (Rowe and Nichols 1980); ** measured from Cherbonnier 1970, fig. 2E–F.

possesses rectal caecae, although a bulging of the rectal canal does seem to occur (incorrectly interpreted as "poorly developed rectal caecae" by Rowe (1985) in a small specimen of *P. polyplax*). Rectal caecae are prominently present in both *P. toyoshiomaruae* and *P. gustavei*. The taxonomic use of this character may be of taxonomic value within the family, although it is known for only three of the five species of *Podosphaeraster*.

Superficially, *P. toyoshiomaruae* appears most closely related to *P. pulvinatus* from Guam and the Loyalty Islands. Although they share the character of bearing many (>20) granules on their abactinal and actinal plates, we consider at least three characters to differ enough to separate the Japanese specimens despite the paucity of specimens for comparison. Table 1 shows that in *P. toyoshiomaruae* skeletal plate granules and adambulacral plate spines increase in number significantly with growth. As far as can be determined at present, *P. toyoshiomaruae* grows to a size of HD/VD=12.2/10.7, but even at that size it bears more granules/spines per plate than either of the known specimens of the larger *P. pulvinatus* (HD/VD=13.4/6.0 [incorrectly cited as 12.75/5.75 in Table 1 of Rowe and Nichols 1980] and 21.5/11.8). *Podosphaeraster toyoshiomaruae* is subspherical at its largest size compared with the distinctly cushion-shaped *P. pulvinatus*. *Podosphaeraster toyoshiomaruae* loses the perforation of the terminal plates with growth whereas the larger *P. pulvinatus* retains the perforations through the terminal plates. Unfortunately, due to lack of suitably preserved specimens of *P. pulvinatus*, gross internal morphology cannot be compared.

Skeletal plates. The basic plate arrangement of *Podosphaeraster* species is typically very distinctive, and little variation is observed in it (Fig. 1; see also Rowe *et al.* 1982, fig. 3; Rowe 1985, fig. 2). The apical system comprises basically one central, five interradial, and five radial plates, although the apical system of *P. polyplax* becomes more extensive and complex by the inclusion of additional plates (Fig. 1). Carinal plates are always four in number. The arrangement of the abactinal and actinal plates, bounded interradially between the apical system, carinal, adambulacral, and oral plates, shows little variation. This arrangement may be described in two ways (see Fig. 1):

a) Following Clark and Wright (1962), Cherbonnier (1970), Rowe and Nichols (1980), Rowe *et al.* (1982), Rowe (1985), and herein: the visually obvious arrangement of eight horizontal rows, though useful taxonomically, cannot be considered to show homology with, or phylogenetic relationship between, any other asteroid, extant or fossil, despite attempts to justify the phylogenetic relationships of *Podosphaeraster*. Blake (1984) has already shown that comparison between *Podosphaeraster* and the superficially similar fossil *Sphaeraster* cannot be sustained.

b) Following Rowe's (1985) alternative interpretation: the arrangement of plates in the less obvious, but nonetheless determinable, longiseries of dorsolateral and actinolateral rows separated by three marginal rows (supero-, infero-, and intermarginals). Rowe (1985: 312) hesitated to argue for his case, although it is clear that this interpretation draws attention to plate homologies and phylogenetic relationships between *Podosphaeraster* and other asteroids. Rowe's (1985) interpretation, if anything, supports recognition of the family Podosphaerasteridae and it's inclusion within the superfamily Goniasteroidea (Goniasteracea therein) as defined by Blake (1987), with closest affinities with the family Goniasteridae.

Digestive system. The digestive system of *Podosphaeraster* is highly special-

ized, with cardiac stomach reduced and the pyloric structure complex compared to those of other asteroid families (Jangoux 1982; Rowe *et al.* 1982; Rowe 1985). The digestive system of *P. toyoshiomaruae* is similar to that of *P. gustavei* (Rowe 1985), with both species having five pouch-like rectal caecae. *Podosphaeraster polyplax* lacks rectal caecae, possessing only a rectal canal that connects the pyloric structure to the anus (Rowe *et al.* 1982). Due to poor preservation of the known material of both *P. pulvinatus* and *P. thalassae*, the internal morphology of these species cannot be compared until fresh specimens have been recovered (Rowe 1985: 318).

Ecology. The ecology of *Podosphaeraster* is poorly known. The collecting localities of *P. toyoshiomaruae* (145–170 m deep) are situated around a top of a small seamount in the Amami Trough (about 800 m deep). The bottom is rough and the bottom current is probably relatively strong. The catches in the dredge included enormous amounts of various sponges and gorgonian and alcyonacean corals. One of the specimens (NSMT E-4568) was collected from a depression in the surface of a demosponge. The other specimens were sorted from dredged material that contained abundant specimens of sponges including in particular the similarly spherical and whitish-colored sponge *Stelletta* spp. (Astrophorida: Ancorinidae). An inference that *P. toyoshiomaruae* is probably associated with sponges seems reasonable. This agrees also with *P. pulvinatus*, which Rowe and Nichols (1980) reported as being found in the branches of a hexactinellid sponge. *Podosphaeraster thalassae* was reported by Cherbonnier (1970) as having been collected from rough, rocky ground. Ailsa M. Clark (in Clark and Downey 1992: 226) commented that the "pea-like size and form" of *Podosphaeraster* seems to make it difficult to collect, accounting for the preservation of usually a few specimens in collections. Its subspherical shape and skeletal rigidity may have led to *Podosphaeraster*'s adoption of a cryptic habitat rather than relying on skeletal strength for protection (Blake 1984), and this may also account for the death of collected specimens.

Distribution. The described species of *Podosphaeraster* are now known to be distributed from off southern Japan, off Guam, in the South China Sea, in the Arafura Sea, and off the Loyalty Islands in the Western Pacific, as well as in the Bay of Biscay and off the Azores in the northeastern Atlantic (Table 2). Ailsa M. Clark (in Clark and Downey 1992) cited an additional specimen (mentioned as personal communication from Downey) collected by a submersible in the western tropical Atlantic, but without specific identity or further details. The depth range for the genus is 85–615 m.

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